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SURVIVAL OF TRANSPLANTED CUPRESSUS IN THE PYGMY FORESTS OF MENDOCINO COUNTY, CALIFORNIA

CALVIN MCMILLAN

In a recent study of the edaphic restriction of *Cupressus* and *Pinus* in central California (McMillan, 1956), certain species from highly acid soils and from serpentine soils were investigated. Soil tolerance studies conducted both under greenhouse conditions and in large outdoor bins were used in this inquiry.

One phase of the investigation not previously reported involved the transplanting of seedling trees to the habitat of the pygmy forest in Mendocino County. At the time of the transplanting no extended analysis of seedling survival was anticipated. Since it has been possible to continue the observations, however, this report will evaluate the survival over a period of seven years.

The pygmy forests have been described adequately elsewhere (McMillan, 1956), but certain features of the transplant site on the coastal plateau between the Little and Albion rivers are pertinent. The transplant area, approximately one mile southwest of the Mendocino County Airport, was on the property of Miss Jean MacGregor Boyd. It had been subjected to previous burnings and was covered by a low growth of trees and shrubs. The site was included within the narrow restriction of both *Cupressus pygmaea* (Lemm.) Sarg. and *Pinus bolanderi* Parl., and both species were represented by numerous individuals varying in height from 25–100 cm. *Vaccinium ovatum* Pursh, *Rhododendron californicum* Hook., and *Gaultheria shallon* Pursh were common shrubs of the area. *Arctostaphylos nummularia* Gray, a species which does not crown-sprout following burning, was represented by a few small shrubs. In adjacent areas with no record of recent burning, *Arctostaphylos* was common with *Pinus muricata* Don. The dense *Sequoia-Pseudotsuga* forest, common on the margins of the plateau, was adjacent to the transplant site. The soil in the transplant garden is a ground-water podsol with a pH of 3.8–4.0. This ashy-colored soil, which is common throughout the areas of the pygmy forest, is usually less than a foot in depth and is one of the most acid soils in California.

Seedlings of the various strains of *Cupressus,* including those of *C. pygmaea, C. goveniana* Gord., *C. abramsiana* C. B. Wolf, and *C. sargentii* Jeps., were transplanted from the greenhouse at Berkeley to the pygmy forest in November, 1950. Six of each strain were planted in each of two series. One group was protected from browsing animals by a large wire screen cage, while the second series remained unprotected. The unprotected seedlings were severely damaged and could not be used in the study. The cage protected the other seedlings throughout the investiga-

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tion. Measurements were recorded at intervals beginning at the date of planting and continuing until August, 1957.

In April, 1952, individuals of the two strains of *C. pygmaea* from Mendocino County (one from the pygmy forest area, the other from Anchor Bay) were dark green and vigorous. Individuals of the two strains of *C. goveniana* from Monterey County (one from Huckleberry Hill and the other from behind Point Lobos) and the one strain of *C. abramsiana* (from Bonny Doone in the Santa Cruz Mountains) were lighter green and lacked vigor. The average growth increment since transplanting showed clearly that the *C. pygmaea* strains were the most vigorous even though the actual increase in height for all strains was slight. Seedlings of *C. sargentii* (from a serpentine area on Mt. Tamalpais in Marin County) were barely surviving in 1952.

Over the same two-year period, seedlings were grown at Berkeley in large outdoor bins containing soil from the habitat of the pygmy forests. These bins were used until 1952 and at that time the responses of the strains reversed the trend indicated in the transplant garden. The vigor and height of the two strains of *C. pygmaea* was less than that of either *C. goveniana* or *C. abramsiana*. In contrast, seedlings of all strains grew well at Berkeley in bins containing an agricultural type of soil. The *C. pygmaea* strain from the pygmy forests was extremely vigorous on the agricultural soil and had an average height of 82 cm. after the 2-year growth period (McMillan, 1956). This contrasts sharply with a 3.3 cm. average height increase of the same strain when transplanted to the pygmy forest habitat.

In August, 1954, the transplant garden was observed after an interval of two years. The growth differential which had been apparent in 1952 was intensified. The trees of *C. pygmaea* were much more vigorous than those of either *C. goveniana* or *C. abramsiana*. Of the surviving strains, only that from Pt. Lobos failed to show an increase in height over 1952 measurements. All of the individuals of *C. sargentii*, the only strain from serpentine soils, had died during the interval.

Observations at the transplant garden in August, 1957, indicated considerable development of both strains of *C. pygmaea*. Somewhat greater vigor characterized the individuals of the pygmy forest strain. Average growth since transplanting was 11.8 cm. The average height increase for the Anchor Bay strain was 9.3 cm. These strains of *C. pygmaea* produced pollen-bearing cones and only the pygmy forest strain had produced a mature seed-bearing cone.

Much less growth and a reduction in the number of surviving trees were noted in *C. goveniana* and *C. abramsiana*. None of the trees of the Point Lobos strain of *C. goveniana* survived. The four surviving trees of the Huckleberry Hill strain had grown very slightly and none was vigorous. Only two of the *C. abramsiana* individuals were surviving and these showed only a trace of height increase.

The growth pattern of dwarfed trees of *C. pygmaea* results from a unique tolerance for the highly acid soils of the pygmy forest area. At the transplant site, small, cone-bearing trees, varying between 25 and 50 cm. in height, had 21 growth rings when measured in 1952. These trees were less than 70 cm. in 1957. Other trees, in pygmy forest areas adjacent to the transplant site, had over 100 growth rings, a 6–10 cm. diameter and a height of less than 2 m. A few larger trees (30–50 m.), such as those measured by Mathews (1929), indicate the type of growth which can be achieved under conditions which support mostly *Sequoia* and *Pseudotsuga.*

Although the survival pattern in *Cupressus* indicates that the strain from the pygmy forests is the best fitted for growth on the highly acid soils in Mendocino County, it must not be inferred that the other strains are incapable of the growth pattern producing a pygmy forest. For example, at Huckleberry Hill, trees of *C. goveniana* closely resemble *C. pygmaea.* Although occasional tall trees of *C. goveniana* occur with *Pinus radiata* Don, the majority of the trees with *P. muricata* give an appearance of a pygmy forest. The inability of the Huckleberry Hill strain to grow well at the transplant garden in Mendocino County is particularly difficult to explain on an edaphic basis because of the marked similarity of the soils of the two areas. Climatic conditions of Mendocino County suggest a more likely explanation. However, trees of *C. macrocarpa,* a species also restricted to the Monterey Peninsula in its natural distribution, are thriving and reproducing along the Mendocino County coast. Unless the climatic tolerances of *C. macrocarpa* and *C. goveniana* differ markedly, the explanation would lie possibly in the action of the highly acid soils in conjunction with the cooler temperatures of the more northern location. Extended periods of freezing temperatures and of dry summer conditions occurred between 1954 and 1957. This may have provided the critical point for reduced survival among all of the strains from the more southerly localities and, in particular, produced conditions beyond the tolerance of the Point Lobos strain of *C. goveniana.* The loss of seedlings of *C. sargentii* early in the study may indicate a low survival potential on highly acid soils by strains from serpentine soils.[1]

Studies of the nature of restriction of *Cupressus pygmaea* indicate that the species is not confined to the pygmy forests because of an inability to grow elsewhere. The restriction results, in part, from the tolerances of *C. pygmaea* for conditions resulting in a dwarfed form and, in part, from the lack of tolerance by taller forms, such as *Sequoia* and *Pseudotsuga,* for growth on the shallow, highly acid soils. Furthermore, these survival studies indicate that *C. pygmaea* possesses a tolerance not shared by the strains of other species of *Cupressus* for conditions of the pygmy forest habitat.

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[1] Preliminary studies indicate that day length factors were not critical in the differential survival of the Huckleberry Hill and Mendocino seedlings. In greenhouse studies, seedlings of the Monterey strain as well as seedlings of both Mendocino strains responded similarly to a range of light periods: 8-hour, 12-hour, and 16-hour.

Selective influences on the coastal plateau of Mendocino County have sorted out a combination of species with unique qualities for survival in one of the most extreme soil situations in California. The pygmy forests which have resulted from this selective action include much of the natural distribution of both *Cupressus pygmaea* and *Pinus bolanderi*. The gigantic *Sequoia-Pseudotsuga* forests which grow in adjacent portions of the coastal plateau present an amazing contrast in vegetational selection.

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AN INTERSPECIFIC CROSS IN CUCURBITA (C. LUNDELLIANA BAILEY × C. MOSCHATA DUCH.)

Thomas W. Whitaker[1]

As one aspect of a comprehensive study of the origin and relationship of the cultivated species of *Cucurbita*, *C. lundelliana* Bailey, a non-cultivated species, was crossed with *C. moschata* Duch., one of the five cultivated species of the genus. In *Cucurbita* successful crosses between truly wild species and domesticated ones have not been hitherto reported. Essentially the cross *C. lundelliana* × *C. moschata* combines two genotypes, the one (*C. lundelliana*) a wild species and the other (*C. moschata*) with a long history of cultivation. The hybridization experiments reported here were made with the idea that the compatability relations might indicate directions in which to search for the common ancestor of the cultivated group, and perhaps suggest in a general way the area where the cultivated forms were domesticated (Whitaker, 1956). Furthermore, it was thought that the results would contribute to an understanding of the heritability of characters such as large fruit, large seed, soft rind, etc., which have value under cultivation. The results reported here provide partial answers to some of these questions.

Materials and Methods

Cucurbita lundelliana, the Peten gourd, is endemic in Central America. It has been collected in Guatemala, British Honduras, and southern Mexico (Yucatan). The plants are strong, vigorous annuals, with fine, wiry stems and deeply lobed leaves having a greyish-green cast (fig. 1B). The flowers of both sexes are large, showy and upright (fig. 1E). The fruits are almost round, dark green, often striped, and have hard rinds, or shells (fig. 2A). The flesh is greenish white and the placenta is solid. The seeds are comparatively small and numerous and have characteristic broad, wavy margins.

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[1] This study was aided by a grant from the American Academy of Arts and Sciences. I am much indebted to Professor Edgar Anderson, Curator of Useful Plants, Missouri Botanical Garden, for helpful suggestions and advice. My thanks are due to G. A. Sanderson, Agricultural Aid, for the photographs and to M. A. McClure, Technician, for preparing figure 4.

Cucurbita moschata cv. Long Genoa Queen is an old and little-known cultivar quite typical of the species. The modern cultivar Butternut of *C. moschata* probably originated as a selection from Long Genoa Queen. The plants have good vigor, large, ovoid leaves, slightly triangular lobed (fig. 1A); long fruits (19 to 36 inches), with an enlarged terminal portion that contains the seeds (fig. 2B). The flesh is dark-orange, moist and slightly stringy.

Both *C. lundelliana* and *C. moschata* have 20 pairs of chromosomes. Unfortunately, it has not been possible to study cytologically the progenies of the cross between them.

Matings of *C. lundelliana* and *C. moschata* cv. Long Genoa Queen produced fruits with numerous fertile seeds. The F_1 proved to be self-fertile and cross-fertile with each parent. In the summer of 1954, the parents and the F_1 were grown in the experimental garden along with several F_2 and backcross progenies. The analysis of the data obtained from the measurements and observations of these progenies constitutes the basis for this report.

Measurements were made of leaf blade length and width, lobe depth and petiole diameter. For male and female flowers the following measurements were obtained: length of corolla, corolla limb, sepal, style plus stigma, staminal column, and ovary length and diameter. Other measurements included fruit length and diameter and length and diameter of several typical seeds. Fruit color, rind hardness, fruit construction, flesh color, and placenta type were also recorded.

The large sprawling plants of most species of *Cucurbita* require extensive space to mature. For this reason it is impractical to raise by conventional methods the number of plants required for a convincing genetical analysis. A more practical method of analysis adapted to the data obtained from this study was suggested by Anderson (1949, 1954), and is the method used herein. Using this method several key characters are chosen for measurement and study, exercising care to select those characters that best represent the differences between the species. Frequency distributions of the scores of each character will indicate in graphical fashion whether the two species overlap in a particular character. More effective in demonstrating the pattern of variation between species is the hybrid index which can be computed from these data. It is designed to show variation of several characters simultaneously. Such an analysis has the advantage of sharply displaying the pattern of differences and resemblances between species, and at the same time suggests how some of the characters that differentiate species are inherited. Stebbins and Ferlan (1956) used this

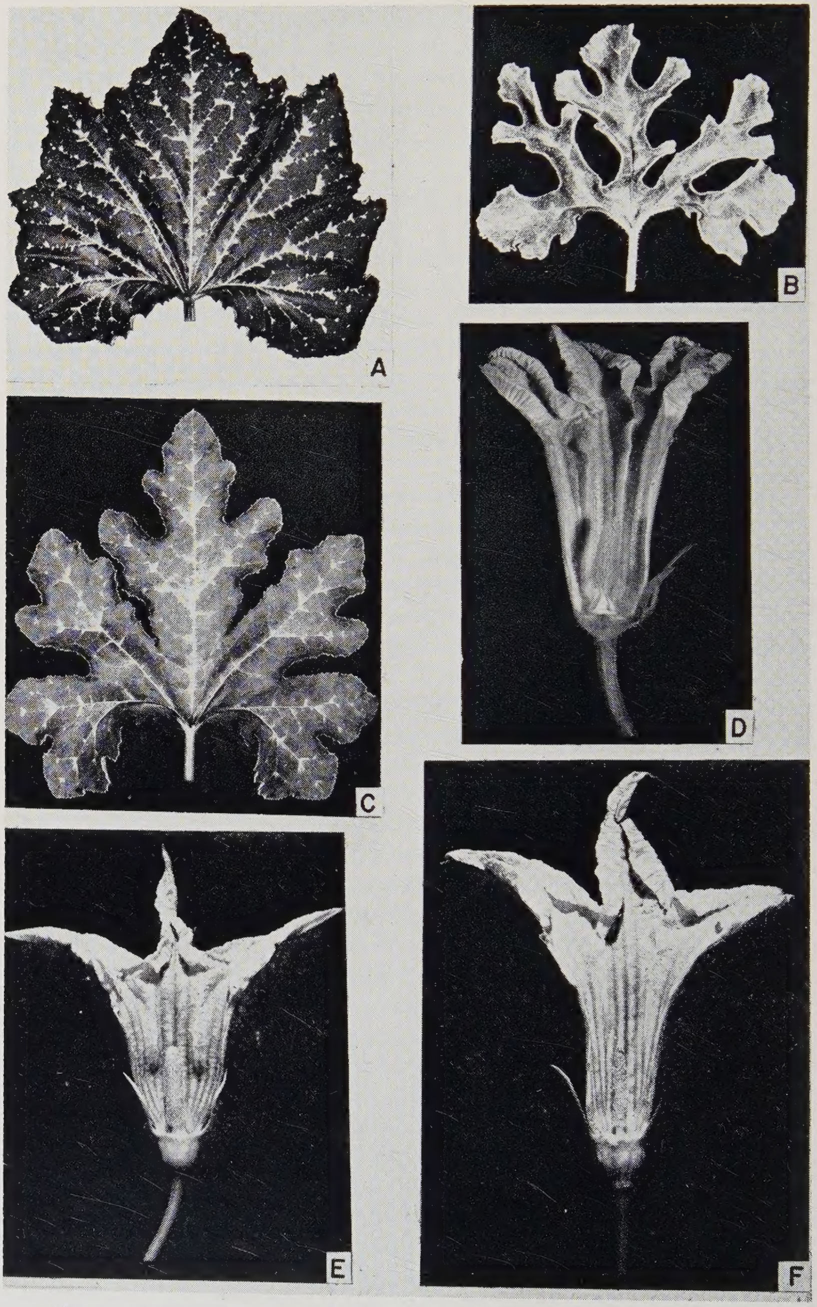

FIG. 1. Leaves and flowers of *C. lundelliana*, *C. moschata*, and F_1 hybrid.

method for investigating the role of hybridization in the origin of intraspecific polymorphism in *Ophrys,* where direct genetic experiments are not feasible for various reasons.

RESULTS

DESCRIPTION OF CHARACTERS USED IN DEVELOPING THE HYBRID INDEX. To treat the measurement and observational data in an objective manner, seven characters were arbitrarily selected for analysis. A hybrid index was computed from data similar to those recorded in Table 1 for the parents. In calculating the values for the hybrid index equal weight was arbitrarily assigned to each character. The character expressions are described as follows.

1. Leaf length / lobe depth. In *C. lundelliana* the leaves are deeply lobed (fig. 1B) as contrasted with the shallow-lobed leaves of *C. moschata* (fig. 1A). This difference is reflected in proportionately larger ratios as the leaf approaches the unlobed condition. The ratios for *C. lundelliana* range from 1.92 to 2.67; those for *C. moschata* from 5.00 to 10.60; and those for the F_1 from 3.00 to 9.00.

2. Leaf width. The leaves of *C. lundelliana* are generally much narrower than those of *C. moschata*. Leaves of *C. lundelliana* range in width from 11.5 to 15.0 cm; those of *C. moschata* from 15.5 to 31.5 cm; and those of the F_1 from 13.0 to 20.5 cm.

3. Petiole. The petioles of *C. lundelliana* are slender and reed-like, while those of *C. moschata* are stouter and more rigid. A measure of this difference is the diameter of the petiole at the point of attachment to the stem. Petiole diameter in *C. lundelliana* ranges from 0.2 to 0.4 cm; in *C. moschata* from 0.7 to 1.0 cm; in the F_1 from 0.4 to 0.6 cm.

4. Length ♂ corolla / length ♀ corolla. In *C. lundelliana* the corollas of the pistillate flowers are usually somewhat longer than those of comparable staminate flowers on the same plant, while in *C. moschata* the corollas of the pistillate and staminate flowers are about equal in length. The ratios for *C. lundelliana* range from 0.41 to 0.80; for *C. moschata* from 0.84 to 1.45; and for the F_1 hybrid from 0.57 to 1.00.

5. Fruit length / fruit width. The fruit of *C. lundelliana* is short and ellipsoidal to almost round (fig. 2A), while that of *C. moschata* is long, slender, with an enlarged terminal portion containing the seed cavity (fig. 2B). Fruits of the F_1 are phenotypically very different from those of the parents and have a constricted neck portion (fig. 2C).

FIG. 1. Leaves and flowers of *C. lundelliana, C. moschata,* and F_1 hybrid. A, leaf of *C. moschata* with shallow lobes and stout petiole; B, leaf of *C. lundelliana* with deep finger-like lobes and slender petiole with long hairs; C, leaf of F_1, which appears to be about intermediate between the two species; D, staminate flower of *C. moschata,* which has short, broad corolla lobes, broad flat sepals, and a stout pedicel; E, staminate flower of *C. lundelliana,* with long, pointed corolla lobes, slender, thread-like sepals, and goblet-shaped calyx tube with slender pedicel; F, staminate flower of F_1, which has the long, lobed corolla, slender sepals and the goblet-shaped calyx of *C. lundelliana* but has a relatively stout pedicel, × 0.48.

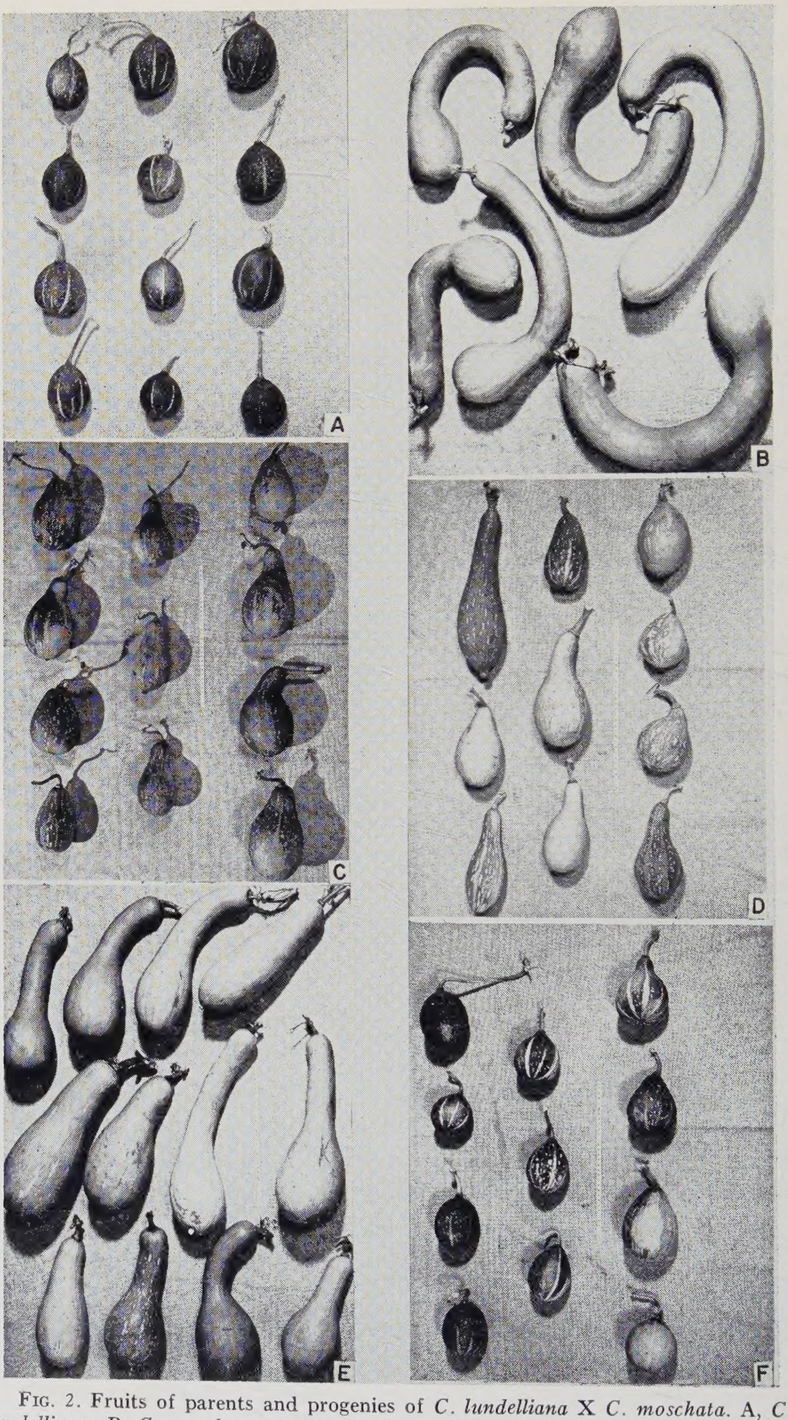

FIG. 2. Fruits of parents and progenies of *C. lundelliana* X *C. moschata*. A, *C. lundelliana*; B, *C. moschata*; C, F_1; D, F_2; E, F_1 backcrossed to *C. moschata*; F, F_1 backcrossed to *C. lundelliana*.

TABLE 1. DATA USED IN COMPUTING AND CONSTRUCTING THE HYBRID INDEX FROM SIX CHARACTERS FOR C. LUNDELLIANA AND C. MOSCHATA*

Species and plant no.	Leaf length / Lobe depth	Leaf width (cm)	Petiole diameter (cm)	Length ♂ corolla / Length ♀ corolla	Fruit length / Fruit width	Seed area (sq. cm)	Index value
C. lundelliana							
5–1	2.56	11.5	0.4	0.71	1.15	0.5	1
5–2	2.27	14.0	0.3	0.64	1.08	0.5	1
5–3	2.17	13.5	0.4	0.54	1.15	0.5	0
5–4	2.36	13.5	0.4	0.52	1.13	0.5	0
5–5	1.92	14.5	0.4	0.41	1.07	0.5	1
5–6	2.67	12.5	0.3	0.52	1.13	0.5	1
5–7	2.60	13.0	0.3	0.50	1.19	0.5	0
5–8	2.27	12.0	0.3	0.60	1.00	0.5	0
5–9	2.50	13.0	0.3	0.63	1.08	0.5	1
5–10	2.50	11.5	0.2	0.75	1.07	0.5	1
5–11	2.33	15.0	0.4	0.58	1.06	0.5	1
5–12	2.30	13.0	0.3	0.80	1.07	0.5	1
C. moschata							
24–1	6.43	15.5	0.8	1.11	4.96	2.0	13
24–2	7.40	21.0	0.7	0.96	6.35	2.0	14
24–3	6.75	30.5	1.0	1.09	7.72	2.0	14
24–4	6.43	25.5	0.7	0.86	4.79	2.0	13
24–5	5.38	25.0	0.8	0.84	4.58	2.0	13
24–6	6.43	24.5	0.7	0.91	5.71	2.0	14
24–7	7.67	26.0	0.8	0.88	6.83	2.0	13
24–8	7.00	23.0	0.7	1.04	5.14	2.0	14
24–9	5.78	31.5	1.0	1.00	7.36	2.0	14
24–10	5.00	25.0	0.8	1.45	6.92	2.0	13
24–11	10.60	30.0	0.8	1.00	5.63	1.5	13
24–12	10.20	28.0	0.7	1.31	5.96	2.0	14

* The seventh character used in computing the hybrid index is not included in the table, since all fruits of *C. lundelliana* have hard rinds and solid placenta, while those of *C. moschata* are non-hard and non-solid. In computing the hybrid index all characters were arbitrarily given equal weight. Each individual was assigned one of three scores for each of the 7 characters; 0=similar to *C. lundelliana*; 2=similar to *C. moschata*; 1=intermediate. Employing this scheme, "pure" *C. lundelliana* =0, while "pure" *C. moschata* =14.

6. Hardness of rind and type of placenta. These two qualitative characters have been combined in the hybrid index. Fruits of *C. lundelliana* have hard, woody rinds that do not decay readily and cannot be cut with an ordinary knife. The seeds are embedded in the solid placenta (fig. 3A, right). *Cucurbita moschata* has a relatively soft rind that can be cut easily even at full maturity, while the placenta is loose and stringy and collapses at maturity leaving a large cavity (fig. 3A, left). The F_1 hybrid (fig. 3A, center) has a hard rind and a more or less open placenta.

7. Seed area. *Cucurbita lundelliana* has relatively small seeds with an area of about 0.5 sq. cm. for each seed (fig. 3B, bottom); *C. moschata* has much larger seeds with an area of about 2.0 sq. cm. per seed (fig. 3B, top). Seeds of the F_1 are about intermediate in area; they range from 0.65 to 1.35 sq. cm. (fig. 3B, center).

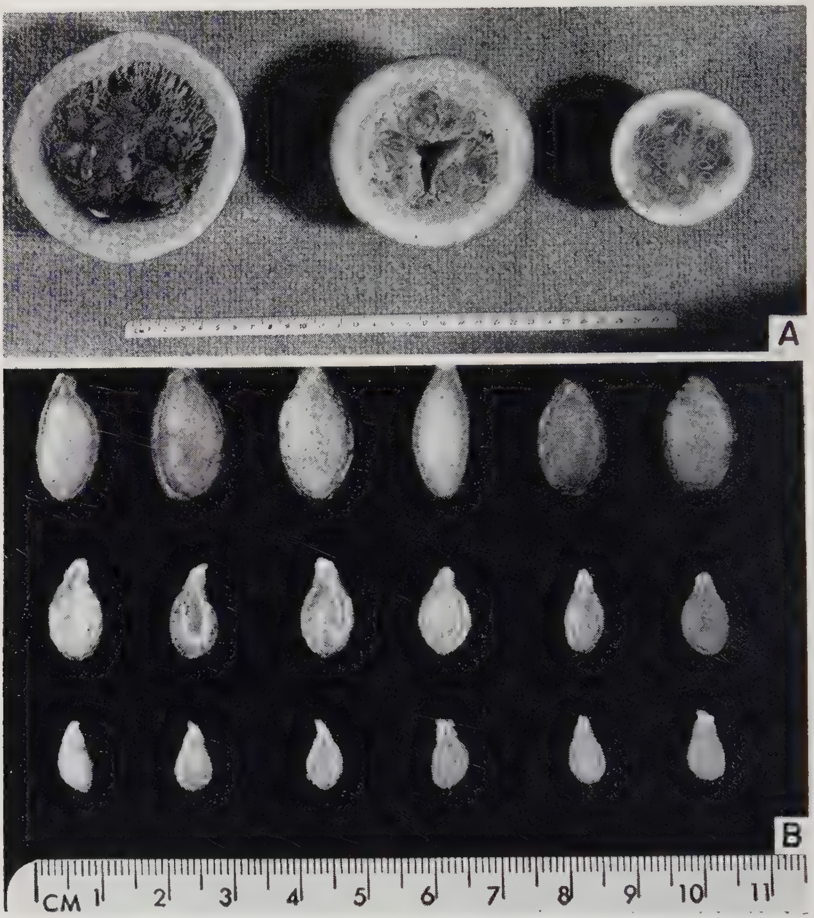

FIG. 3. A, cross sections of fruits of *C. moschata* (left), F_1 hybrid (center), *C. lundelliana* (right); B, seeds of *C. moschata* (top), F_1 hybrid (center), C. *lundelliana* (bottom).

DESCRIPTION OF THE F_1. The F_1 plants were vigorous and thrifty and had foliage somewhat darker green than either parent. An occasional plant in the F_1 progenies had abnormal leaves and stems. Such plants died before producing flowers or maturing fruits. Of the total population of 28 F_1 plants, 7 were male-sterile. The male-sterile plants produced neither abortive nor male flowers. The F_1 plants were approximately intermediate between those of the two species in most characters (see figs. 1 and 2). The frequency distribution of hybrid index values (fig. 4) indicates a minimum overlapping of the F_1 into either species in the characters selected for analysis. There was a wide variation in pollen fertility ranging from 17 to 74%, with a mean of 42% for the 17 plants sampled.

TABLE 2. FERTILITY OF PARENTS, F_1, F_2, and BACKCROSSES OF CUCURBITA LUNDELLIANA X C. MOSCHATA

Parent or progeny	Total plants (number)	♀-Sterile plants (number)	♂-Sterile plants (number)	*Pollen fertility*	
				Mean (percent)	Range (percent)
C. lundelliana	12	0	0	96	85–99
C. moschata	12	0	0	93	80–99
F_1	28	0	7	42	17–74
F_2	27	1	8	39	10–74
Backcross to *C. lundelliana*	72	4	0	76	6–88
Backcross to *C. moschata*	67	0	2?	48	9–94

Description of the F_2. The bulk of the F_2 segregates were more nearly comparable with *C. lundelliana* than with *C. moschata*. In fact, for most characters the F_2 scarcely exceeded the F_1 in the direction of *C. moschata* in our sample of 27 F_2 plants. This conclusion is substantiated by the histogram of the hybrid index values (fig. 4). The different sizes and shapes of fruit produced by the segregates are shown in figure 2D. There were 8 male-sterile plants in the population of 27 plants from 4 progenies. The F_2 segregates were characterized by a wide range in pollen fertility (10 to 74%; mean 39%).

Description of backcrosses. The most noticeable feature of the backcross progenies was their phenotypic similarity to the recurrent parent. In general this was true of vine, flower, and fruit characters. The photographs of the fruits (figs. 2E and 2F) illustrate this point very nicely. The frequency distributions of the hybrid index values (fig. 4) suggest that the population from the backcross to *C. moschata* is more variable than that from the backcross to *C. lundelliana*. Superficially the backcrosses looked as if they might have been slightly more variable populations of either parent.

Fertility of parents and progenies. For the purpose of this study it was important to know something about the fertility of the individuals comprising the F_1, F_2, and backcrosses. Table 2 summarizes the data obtained from field observations and pollen counts.

The data of Table 2 indicate that about one quarter of the F_1 and F_2 individuals from the cross are male-sterile. Plants which did not produce male flowers and those which produced male flowers but aborted prior to anthesis were lumped in this category. It is worth noting that there was not a single clear-cut case of male sterility in the backcross progenies. One plant in the F_2 and 4 plants in the backcross to *C. lundelliana* were males; that is, no female flowers were produced. The pollen fertility of the parent species is very nearly identical (mean 93 and 96%), while the means of the F_1 and F_2 are not very different (42 and 39%). On the other hand the mean pollen fertility for the backcross to *C. lundelliana* was 76% (range 6 to 88%) and that for the backcross to *C. moschata* was only 48% (range 9 to 94%). This sharp difference in mean fertility be-

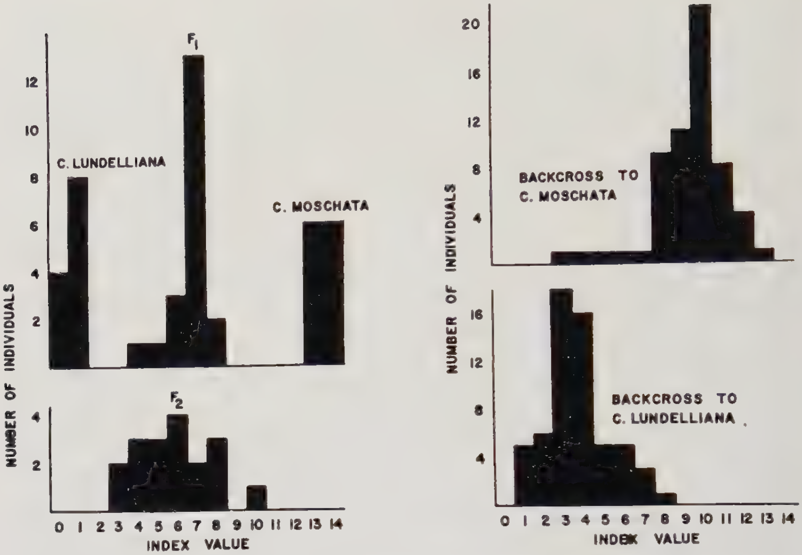

Fig. 4. Frequency distributions of hybrid index values for *Cucurbita lundelliana, C. moschata,* their F_1, F_2, and backcross progenies to both parent species (further explanation in the text).

tween the backcross progenies suggests that maternal or cytoplasmic factors are effective in restoring to a marked degree the pollen fertility of the progenies of the backcross to the maternal parent.

Discussion

The method of analysis chosen for this study has many shortcomings, but it does illustrate certain characters by which the two species differ, and gives a rough quantitative measure of these differences.

The data suggest that some fruit characters, such as large size, soft rind, highly colored flesh, and large seeds, which presumably have value under cultivation, are for the most part recessive. On the other hand, vegetative and flower characters, which in this instance appear to be of less importance under domestication, are intermediate in their expression.

Although the backcross progenies are remarkably similar to the recurrent parent in fruit characters, the frequency distribution of the hybrid-index values (fig. 4) suggests that genes of the other parent are present. The subtle nature of this hereditary contribution cannot be detected except by careful study.

The frequency distribution of the hybrid-index values (fig. 4) indicates that while the F_2 values were considerably more variable than the F_1, as would normally be anticipated, they did not reach values of either of the parent species in the population sampled. The backcross to *C. lundelliana* extends up to the modal class of *C. lundelliana*. However, its own mode is about halfway between the *C. lundelliana* mode and the F_1 mode.

The backcross to C. *moschata* barely reaches the mode of C. *moschata,* and again its mode is approximately halfway between those of the recurrent parent and the F_1.

SUMMARY AND CONCLUSIONS

1. Controlled pollinations demonstrated that a wild annual species of *Cucurbita* (C. *lundelliana*) can exchange genes with a cultivated species (C. *moschata*). The F_1 is fertile enough to produce F_2 and backcross progenies. Individuals of these progenies are fertile in varying degrees except for some male sterility in the F_1 and F_2 generations and for one backcross progeny that had at least 4 individuals that were female-sterile.

2. The parent species are well separated by differences in important morphological characters. This separation is illustrated by frequency distributions constructed from hybrid-index values. From the frequency distributions it is evident that of the 7 characters selected for analysis none are overlapping. The F_1 is intermediate between the parents in the characters selected for analysis except for the qualitative characters—rind hardness and placenta type. An analysis shows that in most characters, the F_2 population barely exceeds the F_1 in the direction of C. *moschata.* This analysis combined with a similar analysis of the backcross progenies suggests that C. *moschata* has many recessive genes.

3. Comparisons of the backcross progenies indicate that they are strikingly similar to the recurrent parent in appearance. This finding suggests that various isolating barriers such as linkage, selective fertilization, and differential viability affect the backcross.

4. If compatibility relations are used as criteria, the isolating barriers that prevent crossing between C. *lundelliana* and C. *moschata* are not well developed in spite of the great morphological diversity between the species. There seems no doubt that each species is a good taxonomic entity. It is equally clear that the two species have a number of genes in common. For this reason it is not unreasonable to suggest that C. *moschata* may have been derived from C. *lundelliana* by isolation and subsequent selection by man. An alternative suggestion would be that both species were derived from a common ancestor, but when domesticated, C. *moschata* diverged sharply by natural selection under the guidance of man.

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THE REPRODUCTIVE STRUCTURES OF SCHINUS MOLLE (ANACARDIACEAE)

Herbert F. Copeland

The *Vergleichende Embryologie der Angiospermen* of Schnarf (1931) has served as the basis and stimulus for very entensive subsequent work in its field. Schnarf accounted for the Anacardiaceae on the basis essentially of a single paper dealing with a single species, being the account of *Rhus Toxicodendron* L. (or *Toxicodendron radicans* O. Kuntze) by Grimm (1912). Subsequent studies of floral morphology and embryology in this family include the following: Juliano (1932) on *Spondias purpurea* L.; Juliano and Cuevas (1932) on *Mangifera indica* L.; Maheshwari (1934) on *Mangifera indica*; Srinivaschar (1940) on *Semecarpus Anacardium* L., *Spondias Mangifera* Willd., and *Anacardium occidentale* L.; Copeland and Doyel[1] (1940) on *Toxicodendron diversilobum* Greene; Sharma (1954) on *Mangifera indica*; Copeland[2] (1955) on *Pistacia chinensis* Bunge; Kelkar (1958a) on *Rhus mysurensis* Heyne; and Kelkar (1958b) on *Lannea coromandelica* (Houtt.) Merrill. The present paper adds *Schinus Molle* L. to the list of species of Anacardiaceae in which the morphology of the reproductive structures is reasonably well known.

Material was collected in the public parks of the City of Sacramento and prepared by routine microtechnical methods (a special technique applied to pollen grains is described below). The results fall short of desired completeness in failing to account for the growth of the pollen tube and for fertilization.

The Tree

Braunton and Davy (1914) tell us that *Schinus Molle* is a native of Peru; that its common name is Peruvian mastic; and that it is very familiar as a cultivated ornamental in southern California, where it has the common name of pepper tree. It is in fact familiar also in northern California, and in many other moderately warm countries.

The tree is fast-growing; of deliquescent form; rarely much more than 10 m. tall; evergreen, with alternate pinnate leaves, the branchlets and leaves often pendant; the small yellow flowers abundant in terminal clusters; dioecious; the female trees producing bunches of purplish-red

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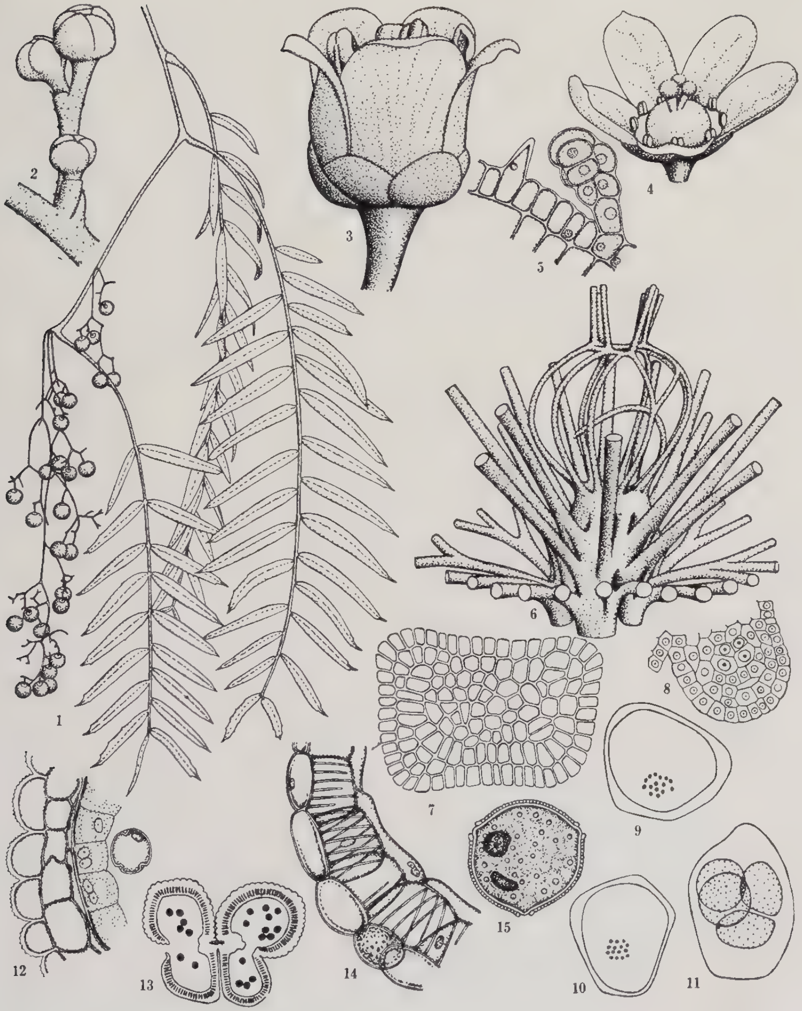
[1] Bernice Elva Doyel, afterward Mrs. Harold Strimling, my pupil, associate, and friend, died in Sacramento on February 24, 1954, at the age of 34 years.

[2] It behooves me to acknowledge, and to call to the attention of readers, a ludicrous error in the paper cited. The median stigma of *Pistacia* is said to stand above the large end of the ovary, in which the ovule is attached. Actually it stands above the small end. Referring to a passage in this paper in the second column of page 442, figures 17, 18, 19, 20, and 21 were drawn with the median stigma to the right; my other figures of the gynoecium and its parts were drawn with the median stigma to the left.



FIGS. 1–15. *Schinus Molle:* 1, fruiting twig, × 0.4; 2, cluster of flower buds, × 8; 3, male flower, × 8; 4, female flower, × 8; 5, pubescence of pedicel, × 320; 6, model of the vascular system of a female flower, × 40; 7, cross section of young anther, × 320; 8, cross section of one lobe of an older anther, × 320; 9, 10, heterotypic metaphase in pollen mother cell, × 720; 11, microspore tetrad, × 720; 12, cross section of wall of developing anther, × 320; 13, cross section of mature anther, × 40; 14, portion of cross section of mature anther, × 320; 15, pollen grain, × 720.

drupes about 5 mm. in diameter (fig. 1). It was the odor and taste of these fruits that suggested the common name of pepper tree.

The pepper tree has not the typical reproductive cycle of plants of temperate regions. It produces flowers continually from spring to fall. It responds to the approach of winter by dropping its flower buds, flowers, and young fruits, and by ceasing to grow until the following spring.

In Sacramento, some of the minute axillary buds give rise to branches at about the beginning of the month of March. Each branch bears first two minute alternate scales, these being the covering of the bud. The axis of the branch elongates during a period of from six to eight weeks, producing from three to seven or more foliage leaves. The terminal bud then produces an inflorescence, or else dies: terminal buds do not normally serve as winter buds. Flowers appear first on a particular tree from the middle of May to the middle of June. They are evidently entomophilous, and honey bees have been seen to visit them. Fruits are mature about two months after flowering: the first ones of the year are found at about the beginning of August.

The axis of a flower cluster, continuing that of a branch, grows in indeterminate fashion, bearing a series of alternate scales, but eventually producing a terminal flower. From the axil of each scale grows an axis bearing, ordinarily, two scales and a terminal flower; from the axils of these scales, in basipetal succession, further growth takes place, usually of a single flower, sometimes of a further cluster (fig. 2). The entire cluster of flowers as described is identifiable as a thyrse.

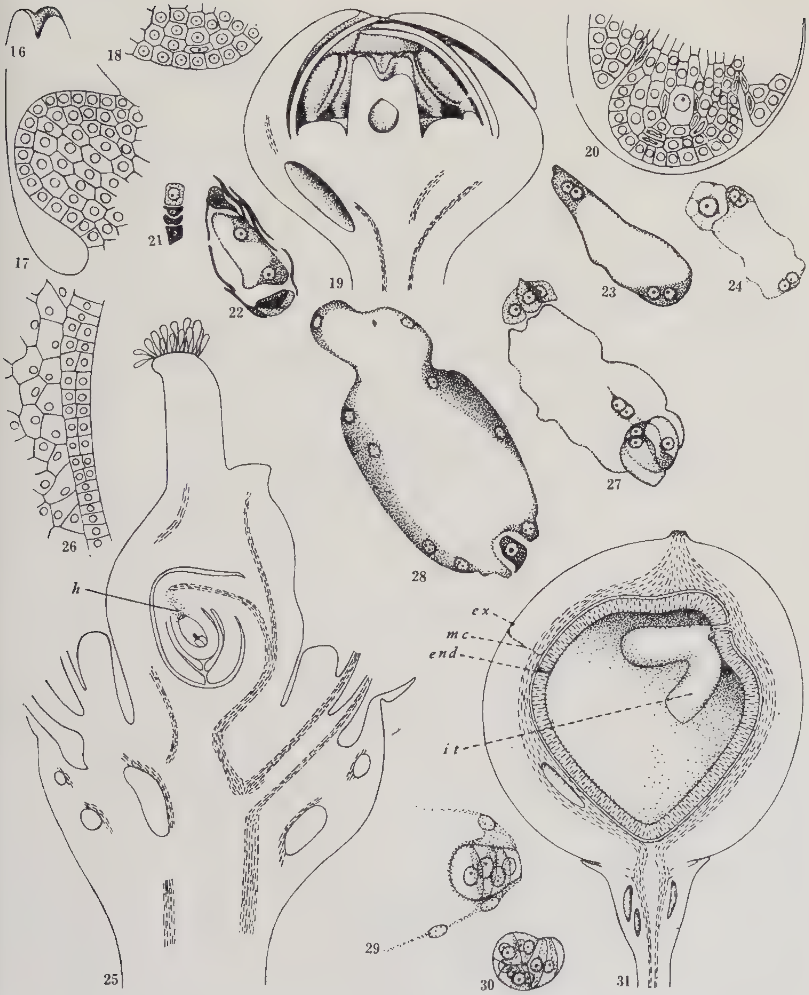
The plant as a whole appears glabrous, but there is a scant pubescence of glandular and simple hairs on the axes and scales of the inflorescence (fig. 5).

FLOWERS

The male flowers (fig. 3) are slightly larger, and have more erect petals, than the female (fig. 4). Each flower has five sepals, five petals, ten stamens, and a pistil. A prominent disk surrounds the base of the ovary inside the bases of the stamens. A small number of stomata are present in its epidermis. The male flowers have minute and incompletely developed pistils; the female flower bear smaller stamens than the male. The sporogenous cells in the anthers of female flowers undergo abortion at the stage of pollen mother cells.

The mature pistil of the female flower is dorsiventral, but not conspicuously so: in the microtechnical operation of imbedding pistils with the intention of cutting sagittal sections, one makes a considerable number of mistakes. The ovary is of a shape approaching that of an egg laid upon its side: it has a larger and a smaller end; a brief style with a terminal stigma stands in a median position toward the smaller end of the ovary; two lateral styles with their stigmas, not particularly different from the median one, stand above the larger end. As a fairly frequent abnormality, pistils occur with only two styles, one above each end. The ovary contains a single locule almost entirely filled by the single ovule. This is attached to the ovary wall in the median plane of the ovary, at the large end, above the middle (fig. 25).

In the phloem of every vascular bundle, but not extending to the ex-



FIGS. 16–31. *Schinus Molle:* 16, longitudinal section of ovary in young female bud, × 40; 17, beginning of development of ovule, × 320; 18, beginning of periclinal division in the nucellar hypodermis, × 320; 19, longitudinal section of female flower bud, × 40; 20, megaspore mother cell, × 320; 21, tetrad of megaspores, × 320; 22, 2-nucleate embryo sac, × 320; 23, 4-nucleate embryo sac, × 320; 24, an abnormality, an embryo sac developing from the spore next to the chalazal spore, × 320; 25, longitudinal section of female flower with a mature embryo sac, × 40; 26, inner epidermis of ovary of open flower, × 320; 27, mature embryo sac, × 320; 28, undivided zygote in plurinucleate endosperm, × 320; 29, 30, young embryos, × 320; 31, longitudinal section of fruit about one month after anthesis, × 8. *h,* hypostase; *it,* tubular outgrowth of outer integuments; *ex,* exocarp; *mc,* mesocarp; *end,* endocarp.

treme end of the bundle, there is a resin duct, conspicuous under the microscope, being of greater bulk than the vascular tissues. The resin ducts enable one easily to follow the course of the bundles.

About five bundles, arranged in a cylinder, ascend the pedicel and enter the receptacle. In the base of the receptacle they fuse and fork to a certain extent, and send out in radial directions branches which undergo further forking. These are the sepal supply; about five bundles enter each sepal. Above their departure, the stele sends out three successive alternating whorls of five bundles, supplying respectively the petals, the sepalad stamens, and the petalad stamens. In male flowers, the vascular tissue ascending beyond the departure of the stamen traces is scant and quickly fades out. In female flowers (fig. 6), much vascular tissue ascends beyond this point. It is of the form of a truncate cone splitting at the summit to form a whorl of bundles whose typical number is eight. One ascends the small end of the ovary; two ascend each side; at the large end there are typically two ovary wall bundles, and between them, or, often, fused to one of them, the bundle which supplies the ovule. At the summit of the ovary, the ovary wall bundles meet and form a scant network. From this network, branches go up into the styles, each style receiving a median bundle and two laterals.

MALE STRUCTURES

The stamens are in all respects of the structure typical of flowering plants. Within the four angles of the rudimentary anther (fig. 7), periclinal divisions occur in the hypodermal cells. The progeny of these cells, produced by duly numerous divisions, become differentiated into the following layers of the anther, in order from outward to inward: (a) the endothecium, the hypodermal layer of cells with ribbed walls, whose contraction opens the anther through two longitudinal clefts (figs. 13, 14); (b) two layers of wall cells, of which the outer becomes compressed, and the inner crushed and absorbed (figs. 12, 14); (c) a tapetum of the secretion type, the cells becoming binucleate and then shrivelling and disappearing (fig. 12); and (d) the spore mother cells. In the male flower, meiosis duly takes place within these last. The haploid chromosome number, observed during this process, is 15 (figs. 9, 10). The pollen grains are separated by simultaneous furrowing. The mature pollen grain (fig. 15) has a wall marked by numerous fine pits and three meridional grooves.

The pollen grains contain much stainable material, and it has been difficult to be certain of the number of nuclei. A technique by which they were made visible was as follows: microtome sections, mounted, deparaffined, and hydrated, were exposed for 20 minutes to 1% Na_2CO_3 to which a little NaOH had been added, at 60°C.; stained briefly with methylene blue; and destained in 95% alcohol. Two nuclei are present. The tube nucleus is the larger. It is subglobular and contains a visible nucleolus. The generative nucleus is smaller, fusiform, and heavily staining. It lies within a distinct space, the generative cell

The Ovule

The parts of the flower originate in the bud in acropetal succession. The pistil, in the female bud, originates as a cycle of three knobs, evidently rudimentary carpels, which, as they grow, become coalescent at the base (fig. 16). Somewhat above the bottom of the cavity in the resulting three-pointed cone, the nucellus begins to grow into it from an area below one of the notches between the points (fig. 17). By further growth, the ovary becomes closed above the locule containing the developing ovule (fig. 19). The points above develop, of course, into the styles and stigmas.

The direction of the axis of the nucellus is at first horizontal or slightly upward. It soon bends and grows diagonally downward. At about this time, the inner integument originates as a collar of tissue surrounding the tip of the nucellus and growing forward with it. The hypodermal cells of a small area near the tip of the nucellus begin to undergo periclinal divisions. One of these cells, near the middle of the area, cuts off to the inside a cell, slightly larger than the others, which is to become the megaspore mother cell (fig. 18). By further periclinal divisions, the megaspore mother cell is carried well to the interior of the nucellus (fig. 20); by growth in other parts, an outer integument is produced; both integuments extend beyond the nucellus and close over it, leaving a small micropyle. At the same time that the growth of the ovule produces these changes, it continues to have a bending or coiling effect: the mature ovule is so bent that its axis points to the ovary wall below its insertion (fig. 25).

Meanwhile, the spore mother cell has produced a tetrad of spores (fig. 21), among which the chalazal spore is functional. The nucleus of the functional spore undergoes three divisions (figs. 22, 23). Six of the resulting eight nuclei are set apart in an egg, two synergids, and three antipodal cells, leaving two polar nuclei in the endosperm mother cell (fig. 27). Thus the embryo sac is of the type which Schnarf designated as normal.

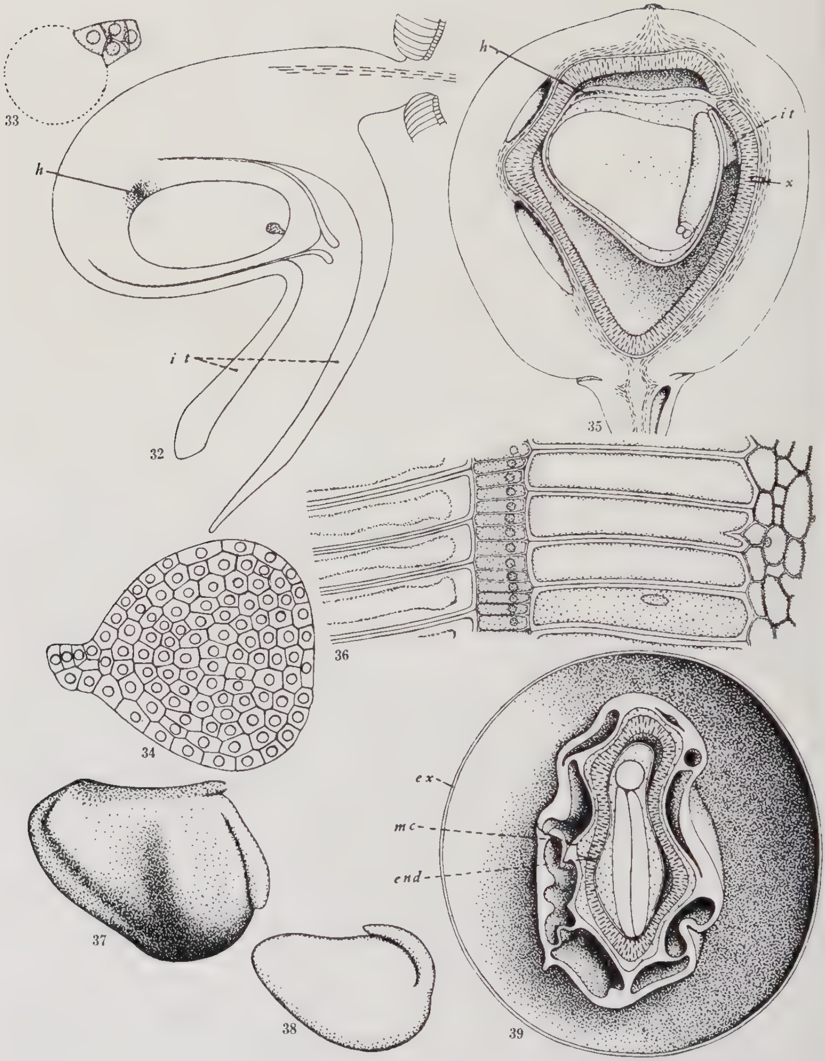
As the embryo sac approaches maturity, there appears in the chalaza, between the end of the bundle traversing the raphe and the antipodal cells, a hypostase (figs. 25, 32, 35), being a body of thick-walled cells of moribund appearance.

A few examples of abnormal development have been noted. An occasional ovule is distorted, twisted otherwise than in the normal downwardly coiled fashion. Sometimes a megaspore other than the chalazal one undergoes development (fig. 24).

Development of Fruit and Seed

The ovary grows during about four weeks after anthesis approximately to the full size of the fruit (fig. 31).

At anthesis, the cells of the inner epidermis of the ovary show periclinal divisions (fig. 26). By these divisions, the epidermis gives rise to three regular layers of cells. The cells of the innermost layer become radially elongate to a length of about 0.2 mm., after which they develop thick



FIGS. 32–39. *Schinus Molle:* 32, longitudinal section of ovule about one month after anthesis, × 40; 33, 34, developing embryos, × 320; 35, longitudinal section of nearly mature fruit, × 8; 36, section of endocarp, area *x* of fig. 35, × 320; 37, mature seed, × 8; 38, mature embryo, × 8; 39, cross section of mature fruit, × 8. *h*, hypostase; *it*, tubular outgrowth of outer integument; *ex*, exocarp; *mc*, mesocarp; *end*, endocarp.

walls. The middle layer becomes a palisade of thin-walled cells, very much smaller than the preceding. The outer becomes a palisade of thick-walled cells, of about the diameter of those of the inner layer, but only about 0.05 mm. long (fig. 36). These three layers, all derived from the inner epidermis of the ovary, make up the stony endocarp of the fruit. Until about a month after anthesis, it is possible to cut on the microtome paraffin sections of the endocarp; later, the thickness and hardness of the walls make this impossible. The endocarp is deeply impressed by the meridional bundles, with their large resin ducts, in the ovary and fruit. As compared with the more or less egg-shaped ovary and fruit, the endocarp is more strongly compressed in the lateral dimension, being approximately lenticular.

During the first month after anthesis, the ovule grows principally in its micropylar-chalazal dimension. The shape of its axis becomes that of a horizontal U: the end of the nucellus points to an area directly below the insertion of the ovule. The outer integument grows forth as a prominent tube, directed downward in the large end of the ovary at right angles to the rest of the ovule. This structure is presumably without function (figs. 31, 32). It persists in a shrivelled condition in the mature fruit (figs. 35, 37).

The endosperm is of nuclear type. It contains a considerable number of free nuclei before the zygote divides (fig. 28). The nuclei remain free when the embryo is 4-celled (fig. 29); when the embryo is of about a dozen cells (at the stage shown in fig. 30), cellular endosperm has begun to form about it. Further uninucleate cells are cut out, first throughout the surface of the endosperm, and then throughout its interior.

The first division of the zygote has not been seen. It occurs about three weeks after anthesis, and is believed usually to be by an oblique wall. The epibasal cell divides, by walls which are usually oblique, two or three more times. Longitudinal divisions then begin, first in the more distal cells, then in the more proximal, but not usually in the basal cell. Thus when a globular embryo is formed (figs. 33, 34), it has a suspensor which is brief and not sharply set apart, consisting of a basal cell which is not enlarged and of one or two pairs of cells beyond this.

After the fruit and its locule have reached nearly their full size, the seed and embryo enter their phase of most rapid enlargement. The seed fills the locule laterally; its end toward the large end of the fruit becomes vertically elongate; it bulges greatly on the side away from the raphe. The impressions in the endocarp, produced by resin ducts, produce impressions on the sides of the seed.

The vertical elongation of the end of the seed toward the large end of the fruit is accompanied by elongation of the hypocotyl and radicle as a stout column in this end of the seed. The root tip points upward, and remains for a long time near the micropyle, but eventually grows past and curves away from it (fig. 38).

The cotyledons grow forth at right angles to the direction of the hypocotyl. They lie in planes parallel to the median plane of the fruit and seed. The raphe increases only moderately in length; the seed coat and endosperm grow forth beyond its end, and the sharp points of the cotyledons extend beyond the hypostase into the pocket thus formed.

The plumule consists of two small knobs placed decussately with respect to the cotyledons.

After the fruit and seed have reached apparent structural maturity, the mesocarp, containing the bundles and resin ducts, becomes shrivelled. A pigmented filmy exocarp, consisting of the external epidermis of the fruit together with one hypodermal layer, encloses a vacant space. Within this, the mesocarp, of gummy consistency, forms a layer on the surface of the stone. A considerable body of endosperm survives in the mature seed (fig. 39).

Discussion

Here one attempts to characterize the Anacardiaceae by their reproductive structures, microscopic as well as macroscopic. Since the microscopic structures are definitely known only of a moderate number of species, most of which belong to the single tribe Rhoideae, the characterization is acknowledgedly tentative.

The Anacardiaceae bear flowers in cymes which are usually gathered into thyrses. They produce imperfect flowers, some species being dioecious, others polygamous. The imperfect flowers usually appear complete through the presence of rudimentary organs. The flowers are pentamerous, except that in most species the gynoecium is of fewer than five carpels. The ovary or ovaries are superior, surrounded at the base by a prominent disk. (To several of these statements, *Pistacia* offers exceptions, evidently through loss of parts.) In the tribe Rhoideae, the pistil is compound, consisting of one fertile and two sterile carpels, with separate styles and stigmas. There is a single locule. A single ovule is attached basally or else to the wall of the locule, on the side away from the mid-plane of the fertile carpel.

Except in the gynoecium, the receptacular vascular system is undistinguished, a matter of the stele emitting alternating whorls of bundles. The sepalad whorl of stamens is the lower. With the reduction of some of the carpels is associated the fact that the ovary wall bundles are not definitely identifiable as carpel dorsals, carpel laterals, and so forth. When the ovule is basifixed, the bundle supplying it is formed by the anastomosis of several or many bundles running together from all sides. This evidently derived character has been noted outside of tribe Rhoideae in *Mangifera* (Sharma, 1954).

Stamens and pollen show no characters distinguishing Anacardiaceae from flowering plants in general. The four pollen sacs open, by the action of a ribbed endothecium, through two slits. The tapetum is of the secretion type: the cells become and remain binucleate, and remain separate until they are absorbed. The most frequently observed haploid chromosome number is 15; Srinivasachar found 14 in *Spondias*. The pollen grains are separated by simultaneous furrowing. They are binucleate. The exine is in many examples marked by numerous fine pits and by three meridional grooves, and contain two nuclei.

Ovule and seed grow in such fashion as to become more or less strongly apotropously coiled in the median plane of the pistil. Basically, the ovule is bitegmous, but various genera exhibit peculiarities in the development of the integuments, particularly the outer. One suggests for future study the possibility that the obturator, the outgrowth at the base of the funiculus which occurs in various genera but not in *Schinus,* may be morphologically a part of the outer integument.

The ovule is crassinucellate. In the area of the tip of the nucellus, there is a hypodermal archesporium, a layer of cells which undergo periclinal divisions. Only one cell of this layer is functionally archesporial: only one megaspore mother cell is produced (these points, not established in our paper on *Toxicodendron diversiloba,* have been observed in subsequently prepared slides of this species). In the chalaza there is present a hypostase, a body of thick-walled cells of moribund appearance.

The embryo sac is of the type which Schnarf designated as normal. Current usage designates this the *Polygonum* type, a term which fails to express what we believe to be its significance.

The peculiar types of development in the integuments are believed to be associated with the occurence of aporogamy, which is definitely known in *Toxicodendron* and *Pistacia*. Double fertilization is presumed to occur, but has been observed only in *Spondias* (Srinivasachar, 1940).

The fruit grows nearly to its full size before the ovule grows considerably, and the ovule grows considerably before the embryo does so. The occurrence of these three distinguishable cycles of growth was noted in *Mangifera* by Kennard (1955).

The fruit is a drupe. In tribe Rhoideae, the endocarp is derived entirely from the inner epidermis of the ovary: it appears regularly to consist of three definite layers of cells; its stony character is produced by the maturation of one or more of these layers as dense palisades of fiber-like cells. These things appear not to be true of *Mangifera* and *Spondias*.

The endosperm is of nuclear type. It becomes cellular first about the embryo, then throughout its periphery, then in all parts.

The first divisions of the zygote are more or less oblique. A brief suspensor, not definitely set apart, or none, is produced.

Enlargement of the ovule in the course of becoming a seed involves considerable bulging on the side describable as the lower, away from the raphe. The raphe does not elongate considerably, but the enlarging seed coat and endosperm push forth beyond the hypostase which marks the end of the raphe. As the growing seed bulges downward, elongation of the hypocotyl-radicle pushes its proximal end downward, while the root tip remains in the neighborhood of the micropyle. The cotyledons lie in planes parallel to the mid-plane of the gynoecium. They grow forth approximately at right angles to the hypocotyl, and their tips extend beyond the hypostase. A certain amount of endosperm survives in the mature seed.

We will be able to recognize other groups of plants as immediate allies of Anacardiaceae whenever we discover in them assemblages of characters showing a family resemblance to the foregoing. Observations of the same nature as these upon further Anacardiaceae should lead to improvements in the system of the family. In the present state of knowledge, it appears that *Schinus* is relatively primitive, and *Pistacia* relatively advanced.

SUMMARY

Schinus Molle, a South American tree popular as an ornamental in California, where it is called the pepper tree, is dioecious. Flowers of both sexes, produced throughout the summer in thyrses, appear complete, but in each the organs of opposite sex are imperfectly developed.

The male parts exhibit no notable peculiarities: endothecium ribbed; tapetum of secretion type, the cells becoming binucleate; haploid chromosome number 15; pollen grains 3-grooved, binucleate.

The pistil is compound, of one fertile and two sterile carpels, with separate styles and stigmas. The single locule contains a single ovule, attached to the wall on the side opposite the style of the fertile carpel. It is apotropous, bitegmous, crassinucellate. A hypodermal layer of archesporial cells in the distal end of the nucellus produces a single megaspore mother cell. The embryo sac is of normal type.

After anthesis, the ovary grows in about four weeks nearly to the size of the mature fruit; ripening requires another month. The fruit is a drupe whose exocarp, of only two layers of cells, encloses, in an empty space, a gummy mesocarp about a stony endocarp. The endocarp is derived entirely from the inner epidermis of the ovary, and consists of three layers of radially elongate cells, two of them with greatly thickened walls.

Considerable enlargement of the ovule is delayed until the fruit is nearly of its full size, and the embryo grows but little until the ovule is in full course of enlargement. The enlarging ovule is marked by a peculiar tube-like extension of the outer integument. The endosperm is nuclear. The first divisions of the zygote are oblique. The suspensor is brief and not sharply set apart from the embryo proper. In the mature seed the hypocotyl points vertically upward in the end of the seed toward the larger end of the fruit; the cotyledons project at right angles from its lower end; a certain amount of endosperm remains present.

Most of these characters are found, by comparison with those of various other Anacardiaceae, to be characters of family Anacardiaceae, or at least of tribe Rhoideae. Groups other than Anacardiaceae will confidently be recognized as related to this family when sets of characters showing a family similarity to these are observed in them.

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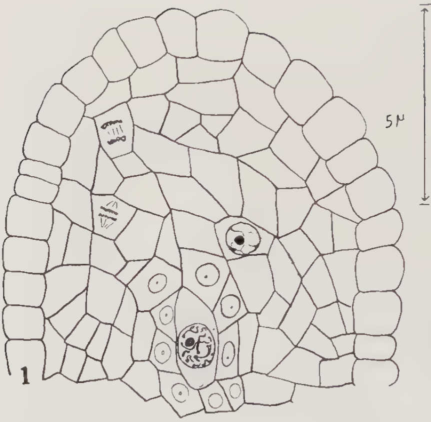
DEVELOPMENT OF THE MEGAGAMETOPHYTE IN LIQUIDAMBAR STYRACIFLUA L.

Franklin F. Flint

No work has been published on the megagametophyte of *Liquidambar*. Within the family (Hamamelidaceae) only two other genera have been studied in regard to megasporogenesis and megagametogenesis (Flint, 1957, 1957A).

Pistillate floral heads of *Liquidambar styraciflua* were collected in Dinwiddie County, Virginia, from March 28 until July 10, 1953. They were fixed in formalin-aceto-alcohol in the proportions of 90 cc. of 70 percent ethyl alcohol to 5 cc. formalin and 5 cc. of glacial acetic acid. Tertiary butyl alcohol, as used by Johansen (1940), was found most satisfactory for dehydration. The heads were then embedded in tissuemat, sectioned at 10-30 microns, and stained with Harris' Hemotaxylin, Safranin O, and Fast Green FCF.

Around 245 ovules are included in this study. Ovules which showed signs of unusual plasmolysis, nuclear degeneration, or had unusually dark staining cytoplasm were eliminated and are not included in the above count.



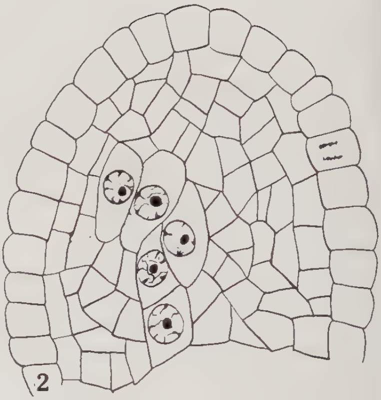


FIG. 1. Young ovule with one megaspore mother cell and one other enlarged nucellar cell. FIG. 2. Young ovule with five potential mother cells. Only one will form megaspores.

MEGASPOROGENESIS

The ovules are formed in two rows within each locule and develop from its base toward the apex. As many as twelve to eighteen ovules are initiated in each locule although only two to six usually form gametophytes and these are most often located near the base of the locule. The ovules may cease development and become degenerate during any stage of megasporogenesis or megagametogenesis.

The megaspore mother cell is first distinguishable within the young ovule, embedded beneath seven to nine layers of nucellar cells. This cell is large, nearly oval in shape, with dense cytoplasm, and a large vesicular nucleus (fig. 1). Frequently as many as five large cells are present within the nucellus and have the appearance of megaspore mother cells (fig. 2). Only one of these cells in an ovule undergoes the meiotic divisions, and it is then that the functional megaspore mother cell can first be determined. In such ovules the functional mother cell is most often located near the center of the group of enlarged cells. After meiosis I is completed, cytokinesis takes place, and a dyad of cells of approximately the same size, each with dense cytoplasm and a large, deeply staining nucleus containing a prominent nucleolus, is formed (fig. 3). The chalazal dyad cell completes meiosis II and cytokinesis takes place, but the micropylar dyad

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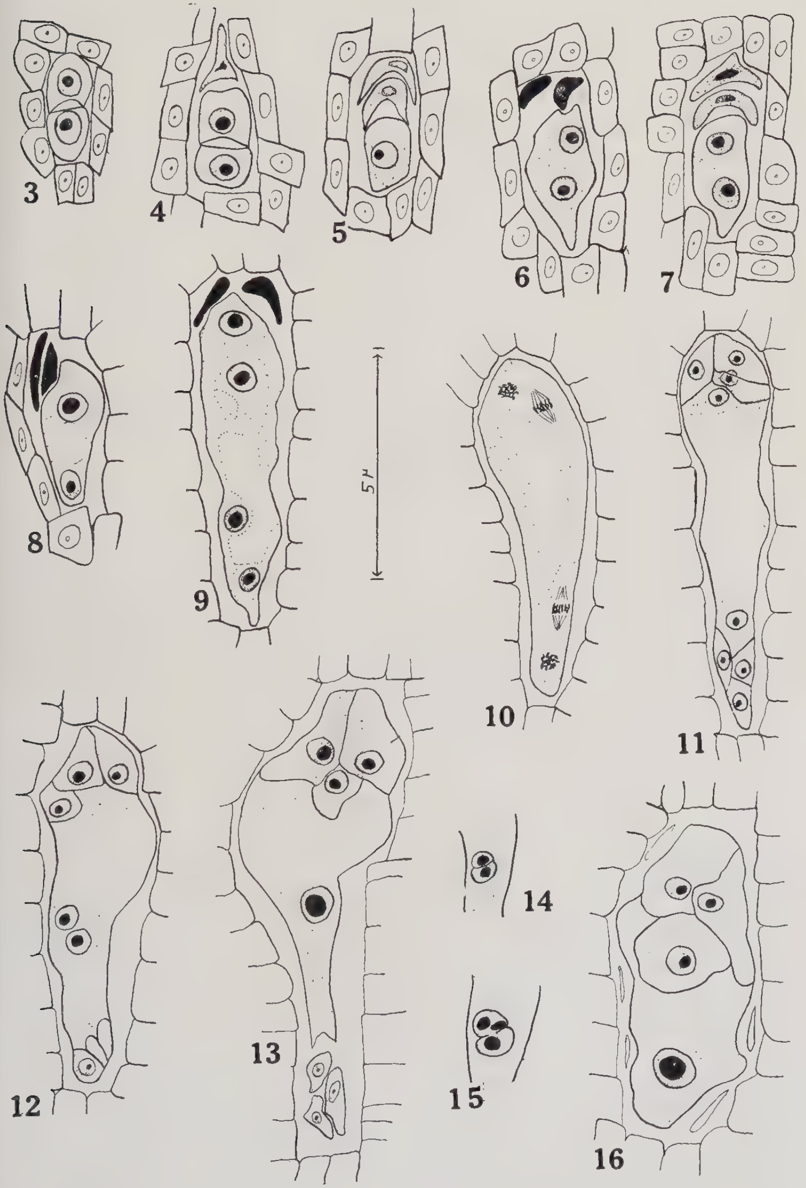
FIGS. 3–5. Megasporogenesis. 3, dyad cells formed from meiosis I of megaspore mother cell; 4, micropylar dyad cell disintegrating while chalazal dyad cell undergoes meiosis II and forms two megaspores; 5, enlarging chalazal megaspore with upper megaspore and micropylar dyad cell disintegrating.

FIGS. 6–16. Megagametogenesis. 6, young 2-nucleate megagametophyte; 7, beginning of vacuoles in 2-nucleate megagametophyte; 8, vacuoles have coalesced in center



of 2-nucleate megagametophyte; 9, 4-nucleate megagametophyte; 10, nuclear divisions to form 8-nucleate megagametophyte; 11, egg apparatus formed, also antipodals, but before migration of polar nuclei; 12, polar nuclei have migrated to center of megagametophyte; 13, polar nuclei have fused and antipodals are disintegrating; 14, fusion of two polar nuclei; 15, fusion of two polar nuclei and sperm nucleus; 16, enlarged egg apparatus of mature megagametophyte.

cell degenerates without undergoing this division (fig. 4). The linear triad of cells which results from this activity consists of the degenerating micropylar dyad cell and the two megaspores formed by the chalazal dyad cell (fig. 4). In all cases observed the chalazal megaspore enlarged further and became the only functional megaspore (fig. 5). The other two cells of the triad are soon pushed aside by the developing megagametophyte which presses them against the surrounding nucellar cells where they gradually disintegrate (figs. 5, 6, 7, 8, 9).

MEGAGAMETOGENESIS

In the ovules studied the chalazal megaspore increases in size, the nucleus divides, and gradually a 2-nucleate megagametophyte is formed (fig. 6). As the cell continues to enlarge, two small lateral vacuoles appear in the cytoplasm, one to either side of the nuclei (fig. 7). Growth of the megagametophyte continues and the two lateral vacuoles coalesce into a single large central vacuole as one of the nuclei and part of the cytoplasm move toward the micropylar end and the other nucleus and remainder of the cytoplasm move toward the chalazal end of the cell (fig. 8). Rapid growth of the megagametophyte continues and each of the nuclei undergoes another division forming a 4-nucleate cell with a pair of nuclei at either end oriented along the major axis of the megagametophyte (fig. 9). The four nuclei undergo a division with one spindle at each end of the megagametophyte oriented along the major axis of the cell and one spindle at each end oriented perpendicular to the major axis (fig. 10). This division results in an 8-nucleate megagametophyte with four nuclei located at either end. The megagametophyte elongates further and the egg apparatus, consisting of three cells, is soon formed at the micropylar end of the megagametophyte (fig. 11). There is no discernible differentiation into an egg cell and two synergids at this time. Three distinct, comparatively large, antipodal cells are formed at the chalazal end of the megagametophyte (fig. 11). The two polar nuclei, one located beneath the egg apparatus and the other directly above the antipodal cells, are immersed in thin cytoplasm and separated by a central vacuole. The polar nuclei soon migrate toward the center of the megagametophyte and lie next to each other (fig. 12). The antipodal cells begin to degenerate (fig. 12) and then separate from each other and the primary endosperm cell (fig. 13). At the same time the micropylar end, containing the egg apparatus, increases in size (fig. 13). The egg cell is soon distinguished from the two synergids by its larger nucleus (fig. 16). The polar nuclei may fuse to form a secondary nucleus (fig. 14) or fusion may be delayed until the sperm nucleus enters, in which case all three nuclei fuse at once to form the primary endosperm nucleus (fig. 15). With the disintegration of the antipodal cells the megagametophyte becomes broader, the single secondary nucleus (or the primary endosperm nucleus, as the case may be) and the egg apparatus enlarge (fig. 16). The cytoplasm of the two synergid cells becomes vacuolated and a small vacuole often appears above the egg nucleus within the greatly enlarged egg cell.

SUMMARY

The megaspore mother cell is embedded beneath seven to nine nucellar cell layers. There are frequently more than one and sometimes as many as five large cells which resemble megaspore mother cells in a single ovule, but only one of these cells functions. A linear triad of cells is formed as the chalazal dyad cell undergoes meiosis II and the micropylar dyad cell does not. In previously studied species of the Hamamelidaceae only one potential megaspore mother cell forms in each ovule and both dyad cells undergo meiosis II to form a linear tetrad of megaspores. The chalazal megaspore develops into the megagametophyte in all species studied. The pattern of development is essentially that of the *Polygonum* type listed by Maheshwari (1950).

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REVIEWS

A Flora of San Francisco, California. By JOHN THOMAS HOWELL, PETER H. RAVEN, AND PETER RUBTZOFF. 157 pp., 20 figs., 1 map. The Wasmann Journal of Biology, Vol. 16, No. 1. 1958. Published in book form by the University of San Francisco. Paper. $3.00.

In spite of the many people now living within the city limits of San Francisco, an amazing number of native plants are still to be found. This is largely due to the hilliness of the city. The hilltops, bluffs, and cliffs provide refuges, many of which have not as yet been commercially exploited. Some habitats, notably the marshes and sand dunes, are rapidly disappearing. On Bernal Heights, however, *Dodecatheon patulum* var. *bernalinum* still grows at its type locality and *Aristolochia californica* is still to be found in ravines near Lake Merced.

In 1892, Katharine Brandegee listed 605 taxa of vascular plants in her "Catalogue of the Flowering Plants and Ferns Growing Spontaneously in the City of San Francisco." Howell, Raven, and Rubtzoff list 1132 species, subspecies, varieties, forms, and hybrids as growing spontaneously in San Francisco now or in the past. Of these, about 42 per cent are introduced plants and about 19 per cent have not been collected since 1940 and are probably now extinct locally. A number of garden escapes are included. Among them are: *Pseudosasa japonica, Pittosporum crassifolium,* 2 species of *Cotoneaster,* 3 species of *Acacia, Albizzia lophantha, Cassia tomentosa, Ruta chalepensis,* and *Buddleia davidii.* The main criterion used for inclusion of a particular garden escape is "whether or not the plant could survive in San Francisco without the aid of summer irrigation." Ample attention also has been paid to weeds. The senior author in particular has collected in disturbed areas in San Francisco, along railroad tracks and in the vicinity of stockyards, and has found such weeds as *Kochia scoparia,* a plant not previously reported from central California. The introduction to the flora contains a short discussion of the vegetation and the geology of San Francisco and a short history of past botanical work on the flora of San Francisco. Descriptions and keys are not provided, but detailed distributional notes are included, and specimens are cited for most species. Authors' names are spelled out in full. The photographs, most of them original, picture typical plant communities, and some of them show the inroads which *civilization* is making into the environment.

This work is a most welcome addition to the existing local floras of various parts of the San Francisco Bay region and will be especially useful to those interested in the distribution and future migration of weeds and garden escapes. It may be obtained at the University of San Francisco Bookstore, San Francisco.—JOHN H. THOMAS, Dudley Herbarium, Stanford University.

Die Nadelgehölze. By GERD KRÜSSMANN. 304 pp., 362 figs. Paul Parey, Berlin and Hamburg. 1955. D.M. 39.60.

The author of "Die Laubgehölze" (Broadleaved Trees) by the same publisher has now made a contribution to the literature on gymnosperms. The term "Nadelgehölze" (Needle-leaved Trees) is used by the author as a traditional convenient term for all gymnosperms, including broad-leaved ones such as *Ginkgo biloba, Agathis* and *Podocarpus.*

Gerd Krüssmann, dendrologist of the Botanical Garden in Dortmund, Germany, is the General Secretary of the International Dendrology Union. A revised edition of Beissner-Fitschen's "Handbuch der Nadelholzkunde" (Handbook of Gymnosperms) was expected after its third edition which was published in 1930. Although the present book does not represent a revision of this well-known "Handbook of Gymnosperms," it answers a great need in dendrology.

Krüssman's book not only emphasizes the gymnosperms hardy in Central Europe, but it also attempts to cover very many other species, varieties and forms that are not hardy in Central Europe. The book is illustrated with excellent line drawings and black and white photographs. The source of each illustration is cited carefully by the author.

The introductory chapter gives a good popular account on the gross morphology of gymnosperms and explains the botanical terminology used for the descriptions throughout the text. This certainly increases the practical value of the book among gardeners, beginners and amateurs. However, some may expect a more proper and careful usage of such terms as "flower" and "fruit" which are generally applied only to angiosperms. The author points out the absence of perianth and ovaries among gymnosperms, but he nevertheless uses these terms freely in the text. "Male" microsporangiate and "female" (ovulate or megasporangiate) cones (strobili) would be the proper terms to apply to the reproductive structures of gymnosperms. Three types of strobili are distinguished under the heading of "Fruits and seeds": 1) Zapfen (cones), 2) Beerenzapfen (berry-like cones), 3) Früchte (fruits). Indeed it is pleasing to note the proper application of the term "berry-like cones" to designate the ovulate cones of *Juniperus* instead of the term "berries" which is a common mistake repeated in various manuals. On the other hand, the term "Früchte" (fruits) is used improperly to designate the fleshy seeds of *Cephalotaxus, Torreya, Taxus, Podocarpus* and *Ginkgo.* A fruit is a matured ovary of an angiosperm, and the usage of the term should be restricted to angiosperms.

The systematic arrangement follows the classification scheme proposed by Professor R. Florin, Stockholm. According to this scheme the Gymnospermae is divided into four classes: Class 1, Cycadopsida, comprises the orders Pteridospermae, Caytoniales, Cycadales, Nilssoniales, Bennettitales, Pentoxylales, Ginkgoales; Class 2, Coniferopsida, covers Cordaitales and Coniferae; Class 3, Taxopsida, includes only one order, Taxales; Class 4, Chlamydospermae, includes one order, Gnetales.

It is interesting to note that this system of classification segregates *Podocarpus, Cephalotaxus* and their allies from the Taxaceae and treats them as separate families such as Podocarpaceae and Cephalotaxaceae under the order Coniferae. The Taxaceae comprises the genera *Amentotaxus, Torreya, Austrotaxus, Nothotaxus* and *Taxus.*

The book gives the descriptions of the orders, families and genera of recent gymnosperms, which are summarized nicely without unnecessary details. The lack of keys seems to be a disadvantage which would render the use of the book somewhat difficult among beginners and amateurs. However, this disadvantage is highly reduced by the comparison of specific differences under each genus, these being presented in beautifully prepared tabular form.

The special part of the book dealing with the descriptions of the genera and species of gymnosperms covers 261 pages in which the genera as well as the species of each genus are arranged alphabetically. The generic descriptions cover gross morphological features of the vegetative and reproductive structures, but also provide some limited information at the anatomical level such as the number and position of resin ducts, vascular bundles, stomatal bands, pollen grains, basic chromosome numbers, etc.

The approximate number of species under each genus is cited in all cases, but I believe some of these figures represent out-of-date information. For instance the approximate number of the species of the genus Pinus is cited as "80 species," which agrees with the citation of Engler and Gilg's "Syllabus der Pflanzenfamilien" (cf. 3rd edition, 1919). Most recent publications accept 90 or more species under this genus. Likewise 40 species are cited for *Juniperus* while other recent publications cite as many as 70 species for this genus. Naturally all newly established species are subject to acceptance or rejection by taxonomists, but I believe that the remarkable increase in the number of species of gymnosperms in recent years is the result of more careful and detailed studies. Therefore this increase is to be expected and should be taken into consideration.

The distribution maps of genera are quite practical and more or less of the same nature as the distribution maps of the genera and families presented in J. Hutchinson's "Families of Flowering Plants." Ranges of distribution and places of main occurrences are also given following the descriptions of genera and species. In some instances the distribution maps disagree with cited ranges and sometimes incomplete data are also obvious. For example the distribution map of the European species of *Abies* taken after Mattfeld is somewhat different from Krüssman's distribution map of this genus. The latter's figure 4 excludes the distribution of *Abies nordmanniana* and fails to indicate the western extension of *A. alba* in Pyrenees. Likewise the distribution of *Torreya californica* is neglected in figure 37 although it is cited under the description of this species on page 285.

Consistent spelling of the locality names would be desirable. "Cilicischen Taurus" appears intermittently with the germanized spelling, "Zilizischen Taurus." Furthermore the usage of ancient, discontinued names of localities should be avoided wherever possible. For example, "Cilicia" of ancient ages has now been replaced by the Turkish name, "Adana."

Rather a large number of gymnosperms of the Pacific Coast of the United States and Canada is included in the book, and therefore it can serve as a good reference to the botanists, students and amateurs of this area. All species of the genus *Abies* along the Pacific Coast are included in the work. With the exception of *Cupressus pygmaea* Sarg. and *C. sargenti* Jepson, all other *Cupressus* species native to the Pacific Coast are taken into account. Furthermore the book comprises all Pacific Coast pines except two recently described species, *Pinus remorata* Mason (1930) and *P. washoensis* Mason et Stockwell (1945). Three-needle pines such as *Pinus attenuata, P. coulteri* and *P. jeffreyi* are listed under the two-needle pines on page 209 erroneously although the cross sectional outlines of their needles on the following page show clearly that they belong to the three-needle section of the genus.

Sequoia sempervirens (Lamb.) Endl. and *Sequoiadendron giganteum* (Lindl.) Buchholz are treated under the same genus although the proposal of J. T. Buchholz regarding the generic segregation of the sequoias is accepted by many in modern literature. The reviewer believes that there are more than sufficient morphological, geographic and ecological differences between the two sequoias to justify their segregation.

The book contains very valuable information on the horticultural uses of different varieties and garden forms of gymnosperms. Those who can correlate the hardiness to conditions of Central Europe with the hardiness to conditions of other geographic areas can make a good use of the knowledge given in the book for judging the suitability of various gymnosperms.

Toward the end of the book a small chapter enumerates the most important pineta in the world. Seventy-seven institutions or localities are listed for eighteen countries in Europe and North America. The author admits the incompleteness of his list and expresses his desire for receiving the recommendations of his readers for the extension of the list. In this connection I would like to suggest the addition of the following arboreta in the United States: Eddy Arboretum at the Institute of Forest Genetics in Placerville, California, which has the most complete living collection of *Pinus* in the world; Westtown School Arboretum in Philadelphia for *Abies* and *Picea*; Morton Arboretum in Lisle, Illinois, for *Picea, Taxus* and *Juniperus*.

The list of literature is short, but it comprises the principal standard references on gymnosperms.

Finally, an index of invalid synonyms of gymnosperms concludes the book. This index is extremely useful to the reader since it clears many confusions in nomenclature.

In general the book is a treasury of information about gymnosperms in spite of its relatively small size. Both the author as well as the publisher deserve congratulations for this valuable publication.—Baki Kasapligil, Department of Biology, Mills College, Oakland 13, California.

NOTES AND NEWS

The second issue of the Index to Plant Chromosome Numbers, compiled from nearly 300 journals published in 1957, is now ready for distribution. There are around 2000 listings of original chromosome counts from the entire plant kingdom and a bibliography of 196 papers from which the listings were taken. Preparation of the Index has been supported in part by a grant from the National Science Foundation of the U.S.A. The price of each issue is $1. Orders for subscriptious may be sent to:

Dr. C. Ritchie Bell
Department of Botany
University of North Carolina
Chapel Hill, North Carolina, U.S.A.

Information on the location and history of any trees of *Cedrus* or *Sequoia* (including *Sequoiadendron*) which were planted in the Pacific coastal states prior to 1900 will be appreciated by E. E. Stanford, Department of Botany, College of the Pacific, Stockton, California.